Spawn and early development of NE Atlantic species of *Hypselodoris* (Gastropoda: Opisthobranchia)

Puesta y desarrollo de especies del género *Hypselodoris* del Atlántico nororiental (Gastropoda: Opisthobranchia)

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SUMMARY

Despite an existing review of the Atlantic species of the family Chromodorididae (Mollusca: Nudibranchia), little is known about early development patterns of these species due to the difficulty of collecting data from living animals. Six species of the genus *Hypselodoris* inhabit the Portuguese continental coasts: *H. bilineata, H. cantabrica, H. fontandraui, H. picta, H. tricolor* and *H. villafranca*. This paper is based on new data and extensive studies made under laboratory conditions and aims to describe several aspects of their reproduction, namely egg mass type, egg size and colour, duration of embryonic development and development patterns. The data here obtained and existing developmental data for Atlantic *Hypselodoris* from the literature are also compared.

RESUMEN

A pesar de que existe una revisión de las especies atlánticas de la familia Chromodorididae (Mollusca: Nudibranchia), muy poco se conoce acerca de la biología y patrones de desarrollo de estas especies debido a la dificultad de obtener datos a partir de ejemplares vivos. Seis especies del género *Hypselodoris* habitan en las costas continentales portuguesas: *H. bilineata, H. cantabrica, H. fontandraui, H. picta, H. tricolor* y *H. villafranca*. En el presente trabajo de aportan nuevos datos obtenidos de estudios en condiciones de laboratorio con el objetivo de describir algunos aspectos de la biología reproductora de estas especies, como el tipo de puesta, tamaño del huevo y color, duración del desarrollo embrionario y patrón de desarrollo. Los datos obtenidos en el presente trabajo se (sintetizan y) comparan con los existentes en la bibliografía.

INTRODUCTION

The Family Chromodorididae (Mollusca: Nudibranchia) comprises one of the most fantastic coloured Nudibranch groups of the Iberian Peninsula East coast. Despite a review (Ortea, Valdés and García-Gómez, 1996) of the Atlantic species of the family Chromodorididae Bergh, 1891 (Mollusca: Nudibranchia), studies specifically devoted to their reproductive biology, from egg

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to metamorphosis are absent. General data on egg mass shapes, egg size or egg-to-juvenile periods are scarce, scattered or absent. Quite often available data come from one single specimen. Furthermore, dispersion measures or confidence intervals are mostly absent.

Like with most aspects of nudibranch biology, there is no general rule concerning their life history and life span. Most species seem to live for about one year, although the tropical Sea hare *Dolabella auricularia* has been reported to live for six years in an aquarium (HADFIELD AND SWITZER-DUNLAP, 1984) and the cephalaspidean *Philine aperta* can live for up to four years in nature (LANCASTER, 1983). On the other hand, there are small nudibranchs, especially those that live and feed on short-lived cnidarian colonies which can complete a life cycle in a few weeks. For example, both the European aeolid *Tenellia pallida* (Alder and Hancock, 1842) [= *T. adspersa* (Nordmann, 1845)] and the coral-eating tropical aeolid *Cuthona poritophages* Rudman, 1979 can mature in three weeks (RASMUSSEN, 1944; RUDMAN, 1979) and probably die within two or three months. In the case of these very short-lived species, they need to complete their life-cycle before the colony they live and feed on dies. If they are too slow then they will themselves die from starvation before they can breed.

Six species of the nudibranch genus *Hypselodoris* inhabit the Atlantic coast of Portugal (CERVERA, CALADO, GAVAIA, MALAQUIAS, TEMPLADO, BALLESTEROS, GARCÍA-GÓMEZ AND MEGINA, 2006): *Hypselodoris billineata* (Pruvot-Fol 1953), *Hypselodoris cantabrica* (Bouchet and Ortea, 1980), *Hypselodoris fontandraui* (Pruvot-Fol, 1951), *Hypselodoris picta webbi* (D'Orbigny, 1839), *Hypselodoris tricolor* (Cantraine, 1835), and *Hypselodoris villafranca* (Risso, 1818).

In this paper we report for the first time data on the spawn and early development of six sympatric *Hypselodoris* species from Portuguese continental coasts maintained under similar laboratory conditions. Several aspects were considered, namely egg mass type, egg size and colour, duration of embryonic development and development type.

MATERIAL AND METHODS

Specimens studied were collected on subtidal surveys using scuba diving in Arrábida (West Coast – 38º 30′ 18″ N, 8º 55′ 18″ W) and the Algarve (South coast-37º 00′ 08″ N, 7º 49′ 20″ W), Portugal, from April 2004 to June 2005. After collection, the animals were brought to the laboratory and placed in closed-circuit 40 L aquaria, where water quality was monitored daily for temperature, pH and salinity, and weekly for the presence of nitrites, nitrates and phosphates. Individuals were kept at a constant temperature (18±1ºC), as similar as possible to that of their natural environment, because egg development timing is known to be strongly affected by temperature; this parameter was kept constant in order to make developmental comparisons. Adults of the same species were kept together and fed with one of their natural prey items, the corneous demosponge *Dysidea fragilis* (Montagu, 1818), which is very common along the Portuguese coasts.

Egg masses were generally laid on the glass walls of the aquaria. The oviposition was considered complete when the adult abandoned the egg mass. Then, the egg masses were carefully removed from the aquaria, incubated individually in 500 L beakers at a constant temperature (18ºC±1) and checked periodically until larval hatching. Extensive observations during embryonic development were made with an optical microscope at regular periods (4-5 times a day) in the centre of the egg mass, in order to register the main development stages before hatching. Daily inspection of all aquaria was necessary to ensure the measurement of zygote diameters before first cleavage since in these planktotrophic species initial development is very fast.

The classification followed for *Hypselodoris* egg masses is the one pro-

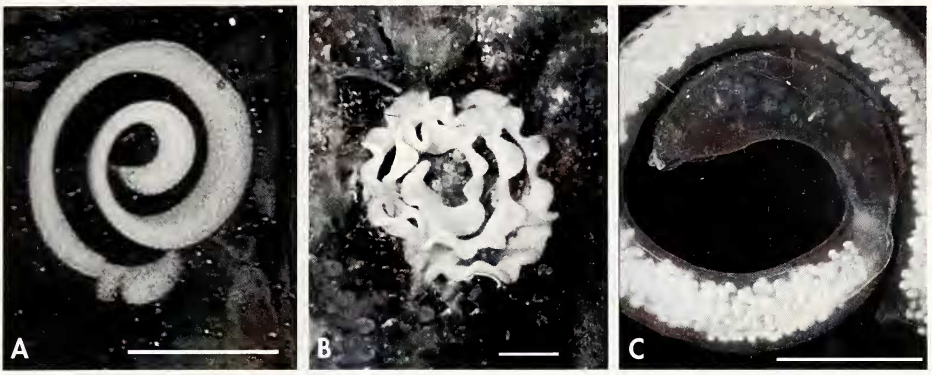

Figure 1. Egg ribbons of *H. bilineata* (A), *H. picta webbi (B),* and *H. villafranca (C).* Scale bars, 2 cm.
Figura 1. Puesta de H. bilineata *(A),* H. picta webbi *(B) y* H. villafranca *(C). Escalas, 2 cm.*

posed by WILSON (2002), which deals exclusively with the family Chromodorididae. According to this author, *Hypselodoris* egg masses are grouped in the following types: A) flat egg masses attached to the substratum by the broad side of the ribbon; B) egg masses with a free edge, shorter or equal than the attached edge causing the ribbon to slope toward the centre or stand upright respectively; C) egg masses with a free edge, slightly longer or much longer than the attached edge, causing the ribbon to slope away from the centre of the spiral or causing ondulations/waves, with an outward slope.

The criteria used to classify the species larval development were those outlined by THOMPSON (1967, 1976): Type 1) planktotrophic development, with a free veliger stage that can be pelagic for an extended period of time and that feeds obligatorily on plankton; Type 2) development with lecitotrophic larvae, with a short-life pelagic veliger that can dispense with plankton feeding due to their large yolk reserves; type 3) direct development, without a free pelagic larval phase.

RESULTS

Egg masses produced in the laboratory by these nudibranchs are identical to those collected in the field. All *Hypselodoris* spp. egg masses are shaped like a spiral ribbon attached to the substratum along one edge and consisting of embryos embedded in a gelatinous matrix (Fig. 1).

Hypselodoris egg masses found are grouped in two types: *H. billineata, H. cantabrica, H. fontandraui, H. picta, H. tricolor* have egg masses corresponding to type C of WILSON (2002), whereas *H. villafranca* have type A ones. Developmental characteristics of the studied species are summarized in Table I.

H. villafranca is the only species studied with direct development. All observed egg masses from this species had embryos passing through a suppressed veliger stage before hatching as benthic juveniles. This form of direct development has been categorized by BONAR (1978) as ametamorphic direct development, which means that this species does not fully develop into a veliger before undergoing metamorphosis.

All other five *Hypselodoris* species studied present a free living planktotrophic veliger, which have similar developmental characteristics. Despite the differences in egg dimensions (Table I), hatching times were also very similar (Fig. 2).

Right after complete oviposition we could often observe two to three different stages of development in the same spawn. The first part to be released could show second cleavage (4 cells), by

Table I. Comparative table of developmental characteristics of species of the genus *Hypselodoris* of the Portuguese Coast, at 18±1ºC. When appropriate, mean measures are given ± standard deviation.
Tabla I. Tabla comparativa de las características del desarrollo en especies del género Hypselodoris *en las costas portuguesas, a 18±1ºC.*

	Geographic range	Egg diameter (µm)	Capsule diameter (µm)	Eggs per capsule	Developmental type	Embryonic period (days)	Length at hatching (µm)	Number of specimens studied
H. bilineata	Eastern Atlantic	73.07±7.19	123.16±9.89	1	Planktotrophic	7,75±0,25	139,5±4,4	10
H. cantabrica	Eastern Atlantic	95.73±8.41	126.96±0.28	1	Planktotrophic	8.25±0.35	161.5±6.0	10
H. fontandraui	Eastern Atlantic	86.41±4.10	135.61±22.15	1	Planktotrophic	7.50±0.14	156.9±5.8	10
H. picta webbi	Caribbean and Eastern Atlantic	171.16±10.52	314.73±41.73	1-2	Planktotrophic	8.04±0.13	219.2±8.3	10
H. tricolor	Eastern Atlantic	85.65±6.97	147.93±25.74	1	Planktotrophic	7.71±0.17	143.2±2.8	10
H. villafranca	Eastern Atlantic, except Canary Islands. Madeira and Azores	243.69±46.06	389.60±45.32	1	Direct	28.00±0.82	515±23	10

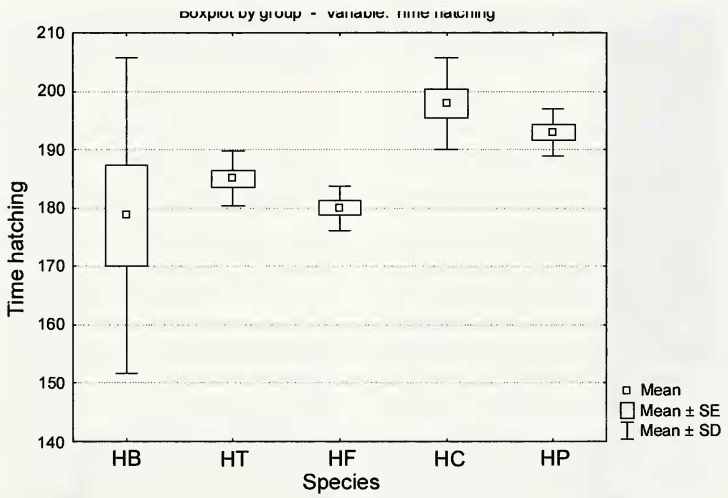

Figure 2- Time hatching duration for all planktotrophic *Hypselodoris* species studied (HB= *H. bilineata*, HT= *H. tricolor*, HF= *H. fontandraui*, HC= *H. cantabrica*, HP= *H. picta*).
Figura 2- Tiempo hasta la eclosión de las especies plAde Hypselodoris estudiadas (HB= H. bilineata, HT= H. tricolor, *HF*= H. fontandraui, *HC*= H. cantabrica, *HP*= Hypselodoris picta*).*

Table II. Overview and timing of embryonic development in species of the genus *Hypselodoris* of the Portuguese Coast, at 18±1°C.
Tabla II. Resumen de la cronología del desarrollo embrionario *desarrollo en especies del género* Hypselodoris *en las costas portuguesas, a 18±1°C.*

	1st Cleavage (hours)	2nd Cleavage (hours)	3rd Cleavage (hours)	Morula (hours)	Blastula (hours)	Gastrula (days; hours)	1st Organs (days; hours)	Veliger stage(days; hours)	Hatching (days; hours)
H. bilineata	2h	4h	7h	12h	17h	1d; 14h	2d; 19h	5d; 20h	7d; 18h
H. cantabrica	2h	4h	8h	13h	20h	1d; 18h	3d; 13h	6d; 4h	8d; 1h
H. fontandraui	2h	5h	7h	14h	17h	1d; 15h	2d; 17h	6d; 1h	7d; 12h
H. picta	2h	3h 30'	8h	13h	25h	1d; 21h	3d; 18h	6d; 6h	8d; 6h
H. tricolor	2h	5h	7h	13h	20h	1d; 14h	2d; 19h	6 d; 1h	7d; 17h
H. villafranca	2h	24h	42h	72h	168h	9 d	11d; 6h	——	28d

the time the later eggs were emerging from the oviduct, still undivided. The stages from morula to blastula were observed during day 0 for all species except *H. villafranca*.

Gastrulation was seen during day 1 except in *H. villafranca*, where it was only observed by day 9. Only after day 5/6 could we designate larvae as true veligers because a shell and a bilobed velum could be clearly seen. In this stage veligers were very active inside the capsules. Duration of the embryonic period from egg to gastrula of all species is presented in Figure 3. The hatching stage occurred between days 7 and 8 after oviposition for planktotrophic species.

The general pattern of cleavage, gastrulation and early embryogenesis of all species examined is typical of that described for other Opisthobranch gastropods (GOHAR AND SOLIMAN, 1967a,b,c). The main embryonic development stages and timings are presented in Table II. Most planktotrophic species of *Hypselodoris* studied present a veliger with a size within the range of 139.5 µm to 161.5 µm. Exception is made for *Hypselodoris picta webbi* veliger which reaches 219.2 µm in length at hatching time. Juveniles of *Hypselodoris villafranca* are dorid-like in shape. They measure 515±23 µm in length at hatching and present a translucent mantle with bright yellow random spots. A structural spicular-like network can be seen in the mantle tissue. This network is maintained in adults of many dorids but is lost in most chromodorids. No eyes or rhinophores buds are visible (Fig. 4). During the first 10-12h post-hatching juveniles crawl on top of the gelatinous matrix of the spawn, sometimes seeming to graze on it.

In Table III we summarise the available information on the developmental characteristics of the studied species.

DISCUSSION

In this study several aspects of the spawn and development of six species of the genus *Hypselodoris* Stimpson, 1855 are described.

The type of egg mass presented by *H. villafranca* is quite remarkable, since it is to our knowledge the first observation of direct development among chromodorids.

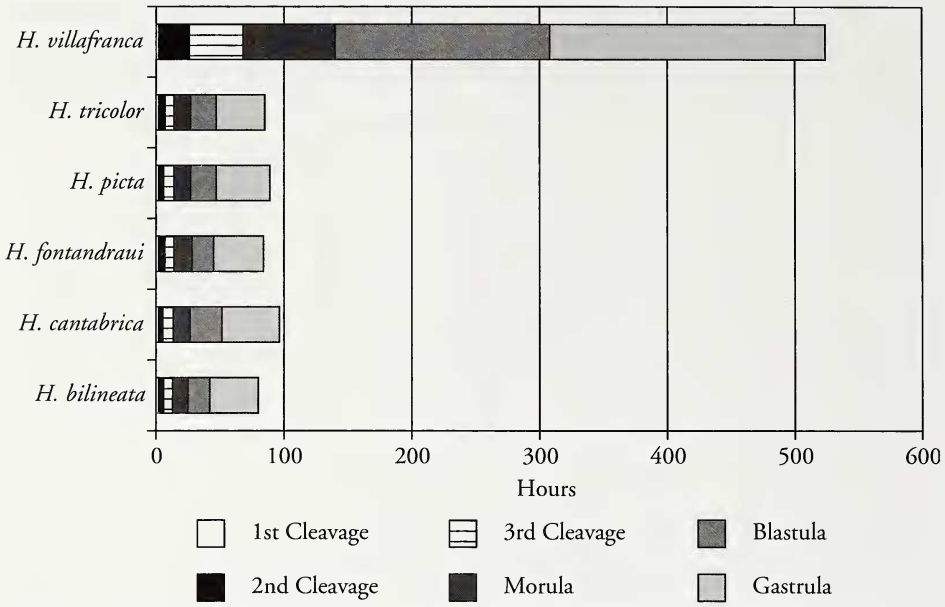

Figure 3. Embryonic period duration from egg to gastrula in all species studied of *Hypselodoris*.
Figura 3. Duración del desarrollo embrionario hasta el estado de gástrula.

Concerning egg size, the mean diameter in *H. bilineata*, *H. cantabrica*, *H. fontandraui* and *H. tricolor* is below 100 µm, within the range reported for most Nudibranchia species (HADFIELD AND MILLER, 1987) and consistent with the planktotrophy exhibited. Egg and capsule sizes are classically considered to be good predictors of development type (HADFIELD AND SWITZER-DUNLAP, 1984) and used for comparative purposes (HADFIELD AND MILLER, 1987). In the case of the Atlantic *Hypselodoris picta*, however, this extrapolation clearly predicts direct development, as in *H. villafranca*, but fails to predict pelagic-lecithotrophy which should be the case of *H. picta webbi* if one follows HADFIELD AND SWITZER-DUNLAP's (1984) predictions. The same situation was reported by THOMPSON (1967) for *Archidoris pseudoargus*, a planktotrophic developer whose eggs are 170 µm in diameter. A free-swimming, planktotrophic veliger can emerge from eggs of very different sizes, from 73 µm in *H. bilineata* (average adult length 30mm), to 171 µm in *H. picta webbi* (average adult length 100mm). The latter is the largest planktotrophic egg size reported so far among nudibranchs (see TODD, LAMBERT AND DAVIES, 2001 for a review). Clearly the amount of energy packed into each ovum is very different. Nevertheless, survivorship and time to competence in these larvae remains unknown. The difference in hatching time between species with planktotrophic larvae and the one with direct development is certainly due to developmental constraints. Even so, the total egg-to-juvenile period is generally longer and variable in the planktotrophic strategy since it is dependent of an external source of energy to undergo metamorphosis (TODD, 1983; HAVENHAND, 1993).

One of the reasons for supporting egg size with capsule size data, in order to have a more accurate development extrapolation (CLARK AND JENSEN, 1981; HADFIELD AND MILLER, 1987) is the fact that there are species with lecithotrophic or even direct development although

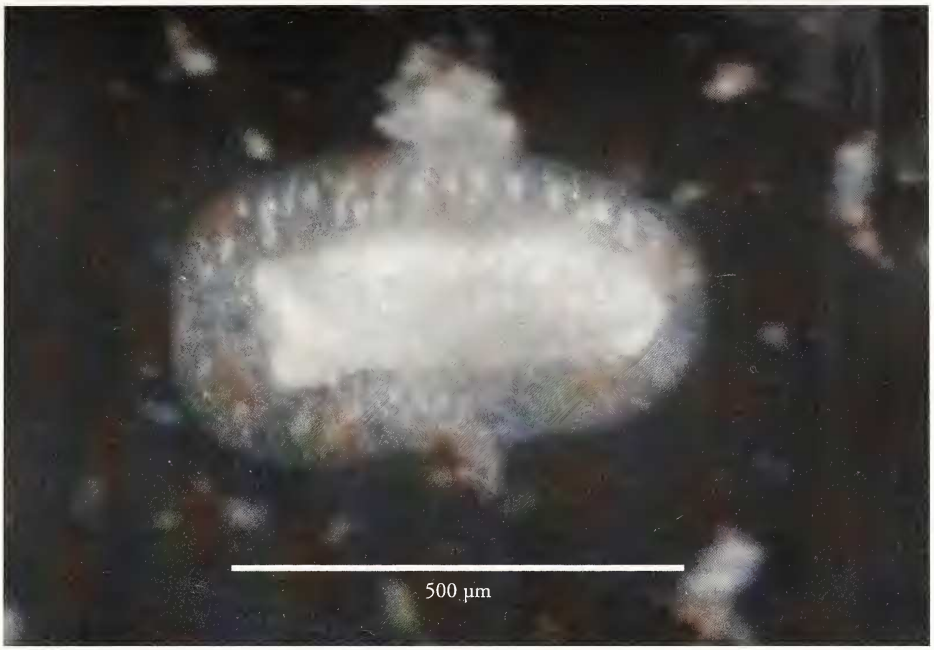

Figure 4. Newly hatched juvenile of *H. villafranca*.
Figura 4. Juvenil recién eclosionado de H. villafranca.

having small eggs. This is common among Sacoglossa species as stated by JENSEN (2001). The situation can be explained based on the presence of albumen, an intracapsular substance rich in proteins and very common in Opisthobranchia spawns (CLARK AND JENSEN, 1981) and the existence of extracapsular yolk in some species, which gives additional nutritional support for embryos, larvae and juveniles (MARIN AND ROS, 1993).

All studied species show a holoblastic and spiral cleavage, typical of the Gastropoda group (BIGGELAAR AND HASZPRUNAR, 1996). With the exception of *H. villafranca* with its slower direct development, all species reach morula stage 12-14h after oviposition and gastrula stage before the 48h mark. Both planktotrophic and direct development species gastrulate by emboly, as described for *Dendrodoris and Chromodoris* by GOHAR AND SOLIMAN (1967a,b) and for *Platydoris* by SOLIMAN, (1978).

The development from gastrula stage to veliger, with all typical structures present lasts between 102-107h.

It is obvious that Opisthobranch life-cycle and developmental strategies are inextricably linked to adult food specificity. Species that feed on transient food organisms are usually small and present a short life cycle, with a very rapid embryonic development. On the other hand, species, like the *Hypseloris* here presented, that depend on large long-living colonies such as sponges, are often bigger in size and have longer life cycles with slower embryonic development (RUDMAN AND WILLAN, 1998).

Although some developmental timetables have been reported for a number of opisthobranch species, it is often difficult to use them to make comparisons due to uncontrolled husbandry conditions or severe differences in water culture temperature, which is known to be one of the key factors affecting embryonic development.

Table III. Summary of developmental characteristics of Atlantic species of the genus *Hypselodoris* from available literature and present study.

SPECIES	Type of egg mass	Egg mass color	Egg mass width (mm)	No. of specimens	Type of capsule
H. bilineata	1 whorl spiral ribbon	White	3	-	-
	Spiral ribbon	White	-	-	-
	3 whorls ribbon	Red-orange	5	1	-
	2 Whorls spiral ribbon	White	4		
	2-2,5 Whorls Spiral ribbon	White	3	7	Oval
	2 Whorls spiral ribbon	White		8	Spherical
H. cantabrica	4 whorls spiral ribbon	White	-	-	-
	Spiral ribbon	White	-	1	Oval
	Spiral ribbon	White		1	
	4 whorls spiral ribbon	White		10	Oval
H. fontandraui	Spiral ribbon	White	-	-	-
	Spiral ribbon	White	-	-	-
	Spiral ribbon	White	-	1	-
	2 Whorls spiral ribbon	White	-	10	-
H. picta webbi	Waved spiral ribbon	Red-orange	6	-	-
	Smoothly waved spiral ribbon	Orange	-	-	-
	5 Whorls waved spiral ribbon		10	1	-
	4 Whorls waved spiral ribbon	Pink-orange	-	-	-
H. tricolor	3 whorls spiral ribbon	White	2	-	-
	Spiral ribbon	White	-	3	Spherical
	2.5 Whorls Spiral ribbon	White	3	5	-
	2 Whorls spiral ribbon	White	-	-	-
H. villafranca	2 Whorls spiral ribbon	Orange	2.5mm	-	-
	Spiral ribbon	Orange	-	2	Oval or spherical
	1 whorl spiral ribbon	Orange			Spherical

The studies on development presented by MARTÍNEZ-PITA, SÁNCHEZ-ESPAÑÑA AND GARCÍA (2006) on species of *Polycera*, conducted at 19°C, report similar embryonic stage timings to those presented for planktotrophic species of *Hypselodoris* in the current study. YONOW (1996) cultured *Acteon tornatilis* at 12°C water temperature and noted that the 4-cell stage was reached about 24h after oviposition and the gastrula stage within 4.9-6d. Although there are no significant differences in development pattern between compared species, these last data report a much slower embryonic development than our study, which is probably due to the 6°C difference in water temperature.

All *Hypselodoris* planktotrophic species exhibit a similar embryonic growth pattern and despite differences in egg size no differences are registered for hatching times. *Hypselodoris picta webbi* presents the biggest veliger (219.2±8.3 µm) but this size discrepancy with other planktotrophic species seems to be more related to adult size (approximately 100mm length) than to any developmental pattern. Nevertheless, survivorship and time to competence in these larvae remains unknown.

When hatching, morphological resemblance of *Hypselodoris villafranca* crawling juveniles to adult specimens is very limited and no rhinophores are visible. The crawling behaviour that the juvenile exhibits for 10-12h on top of the gelatinous matrix of the spawn, seeming to graze on it, leads us to think that matrix nutrients are not only important during embryonic development but

Tabla III. Resumen de las principales aspectos del desarrollo de las especies atlánticas del género Hypselodoris *obtenidas a partir de la bibliografía y del presente estudio.*

Capsule diameter (μm)	No. of eggs per capsule	Egg diameter (μm)	Embryonic period in days	SOURCE
10^-120	-	79-109	-	Ortea *et al* (1996)
110-120	1	-	-	Garcia Gómez (2002)
-		175-208	-	Bouchet and Ortea (1980)
120	1		11 (18-20°C)	Gantes (1962)
158(±3,5)l	1	85-100	9 (21°C)	Sánchez-Tocino *et al* (2007)
100-133	1	67-100	7.75±0.25	Current Study
-	-	95-125	7 (22°C)	Ortea *et al* (1996)
90-140	1	-	-	Garcia Goméz (2002)
95-125	1	80-85		Sánchez-Tocino *et al* (2007)
117-144	1	75-120	8.25±0.35	Current Study
150-180	-	110-120	-	Ortea *et al.* (1996)
150-180	1	-	-	Garcia-Gómez (2002)
145-180	1	110	13 (18°C)	Sánchez-Tocino *et al.* (2007)
95-233	1	80-100	7.50±0.14	Current Study
-	-	175-208	-	Ortea *et al* (1996)
160-190	1	-	-	Garcia-Gómez (2002)
170x200	1-2	130-135	-	Sánchez-Tocino *et al.* (2007)
240-453	1-2	141-210	8.04±0.13	Current Study
90-120	-	85-100	13 (20-22°C)	Ortea *et al.* (1996)
90-120	1	-	-	Garcia-Gómez (2002)
170x200	1-2	130-135	-	Sánchez-Tocino *et al.* (2007)
85-181	1	71-90	7.71±0.17	Current Study
300-400	-	Bit smaller than capsules	-	Ortea *et al.* (1996)
320-360	1	-	-	Garcia-Gómez (2002)
300-599	1	173-430	28.00±0.82	Current Study

serve as first food for juveniles after hatching (GIBSON AND CHIA, 1991).

Although some work is still required to understand some of the differences here recognized in development patterns between these species, the data presented in this work with a systematised character and controlled husbandry conditions of specimens, will certainly be useful regarding potential taxonomic or phylogenetic discussions.

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